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**IMPORTANCE OF ESTUARINE REARING TO CENTRAL CALIFORNIA
STEELHEAD (*ONCORHYNCHUS MYKISS*) GROWTH AND MARINE
SURVIVAL**

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ABSTRACT

Estuaries are important rearing areas for many juvenile fishes and invertebrates. Often viewed as nursery habitats, estuaries are productive waters affording high growth potential and protection from predation. Juvenile anadromous salmonids move through estuarine waters during their annual migration from stream habitats to ocean waters where maturation occurs. In central California, near the southern extent of the steelhead (*Oncorhynchus mykiss*) range, estuaries often form seasonal freshwater lagoons, primarily during summer low flow conditions. To investigate the role that estuaries play in southern steelhead survival, I monitored juvenile size and growth and size at ocean entry of returning adults in Scott Creek, a representative central California coastal stream. During the annual spring emigration, the largest smolts (>150 mm fork length) move directly to sea, while some of the smaller smolts remain in the estuary until sandbar formation creates a closed freshwater lagoon. They remain in estuarine habitat at least until bar breakage during winter storms. High growth rates in the estuarine lagoon throughout the summer result in a doubling of fork length from the time of estuary entry (mean FL of spring migrants-112 mm, mean FL of fall lagoon resident-206 mm). Morphological analysis of returning adult steelhead scales indicates that there is strong size-dependent mortality at sea. Based

upon tagged recaptures and scale samples, estuary-reared steelhead show a large survival advantage and comprise 85% of the returning adult population despite being between 8% and 48% of the juvenile population. Although the Scott Creek estuary comprises less than 5% of the watershed area, it is critical nursery habitat, as estuary-reared juveniles make a disproportionate contribution to the spawning adult pool.

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INTRODUCTION:

Pacific salmon, including both semelparous salmon and iteroparous steelhead, are born in freshwater rivers and streams, and eventually move to the ocean to grow and mature before returning as adults. Because of their anadromous nature, salmonids inherently encounter several distinctly different habitats throughout their life-history. The effects of differential habitat use on growth and survival of individuals may play large roles in their recruitment to the adult population, and has been the focus of extensive study (Reimers 1973; Mitro and Zale 2002; Harvey et al. 2005).

During their seaward migration salmon may enter estuarine habitats, which vary widely in their physical characteristics (Healey 1991). Estuaries are of particular interest because they have been found to be nursery habitats for many species of fishes and invertebrates (Sogard 1992; Yamashita et al. 2000; Epifanio et al. 2003; Le Pape et al. 2003; Brown 2006). These nurseries provide a productive area that allows juveniles who use them to recruit disproportionately to the adult population compared to those from other habitats, because of the increased growth and survival nurseries afford (Beck et al. 2001). Salmon utilizing estuarine habitats have been well documented for rivers from British Columbia to central California (Reimers 1973; Levy and Northcote 1982; Dawley et al. 1986; McCabe et al. 1986; MacFarlane and Norton 2002). However, the time spent in an estuary, and the benefits received from that habitat may vary widely among species and watersheds. Some salmon move through estuaries in days, while others remain for months (Reimers 1973; Myers and

Horton 1982; MacFarlane and Norton 2002; Miller and Sadro 2003; Bottom et al. 2005).

Several theories have been proposed to explain why salmon may choose to remain in estuarine waters, postponing their eventual ocean migration. Estuaries can be extremely productive and may provide excellent opportunities for growth due to a complex invertebrate prey community and warmer water temperatures that cannot be found in freshwater tributaries (Boehlert and Yoklavich 1983; Macdonald et al. 1987; Shreffler et al. 1992). Estuaries may also provide a habitat where young salmon can avoid predation because visual predators may be limited by the potentially turbid nature of estuarine waters (Simenstad et al. 1982; Gregory 1993; Thorpe 1994)). Finally, because the physiological adaptation from a freshwater to a marine environment can be energetically costly, the estuary may provide a transition zone where fish can acclimate to increasing salinity before entering the ocean (Iwata and Komatsu 1984).

Estuaries of smaller coastal watersheds in the southern margin of North American Pacific salmon and steelhead distributions commonly form ephemeral freshwater lagoons. These lagoons are the products of low summer flow regimes that cannot displace ocean sand deposition at the estuary mouth. Eventual formation of a sandbar effectively blocks surface connectivity with the ocean, and reduces the tidal influence on the system, creating a warm, mostly freshwater, slow moving body of deep water. Summer temperatures in these systems can be substantially greater than temperatures in upstream tributaries, and may at times be near the thermal tolerance

limit of steelhead (~25° C) (Myrick and Cech 2004). Lagoon conditions are generally present until the first winter freshet¹ increases stream flow and removes the sandbar, opening the estuary to the ocean. The development of lagoon conditions and their effects on salmonids is not well understood, although a recent study has shown a lagoon² environment to be beneficial to the growth of steelhead in central California (Hayes, unpublished data). Steelhead hatch in upstream waters and tributaries of creeks and spend some portion of time there before migrating toward the ocean. Many move quickly through estuary and enter the ocean, while others remain in the estuary habitat for an additional 6-9 months before ocean entry.

Throughout much of their range, steelhead populations continue to decline despite a federal Endangered Species Act (ESA) listing. This loss has been attributed to habitat loss, water loss and poor land management (Nehlsen et al. 1991; Busby et al. 1996). Still, the factors effecting steelhead population dynamics are not well understood, and few studies have looked at juvenile rearing habitats and their effect on survival for these threatened populations. Ward and Slaney (1989) found a strong size-dependent ocean survival in British Columbia's Keogh River steelhead, with the largest smolts exhibiting a higher survival than the smaller migrants. In their landmark study of central California coastal steelhead, Shapovalov and Taft (1954) suspected the Waddell Creek estuary as potential beneficial rearing habitat:

¹ A freshet refers to the sudden large increase in stream flow resulting from locally heavy rains.

² To avoid confusion, further reference to the physical space that forms either an open estuary in the winter and spring, or closed lagoon in the summer and fall is referred to as estuary habitat regardless of its condition.

“It is possible that the fish of the age 1 group have a strong tendency to stay in the lower stream and lagoon in order to make use of the extremely favorable living conditions there, while the fish of the age 2 group have reached a size where they can most favorably make use of the growing conditions found in the ocean.”

However, neither Ward and Slaney (1989), nor Shapovalov and Taft (1954) were able to attribute survival of returning adults to a particular juvenile rearing habitat. Although young steelhead have been observed in estuaries (Dawley et al. 1985; Quinones and Mulligan 2005), the effects of that habitat on juvenile-to-adult survival has not been evaluated. Higher ocean survival of estuary-reared steelhead would implicate the estuary as an important nursery habitat despite its small proportion of all freshwater habitats. In light of population declines it is necessary to make the link between individuals that recruit to the reproductive population, and the factors that may have lead to their survival.

In this thesis, I address several questions to determine whether coastal California estuaries may serve as juvenile steelhead nursery habitats: *Do steelhead from Scott Creek exhibit evidence of size-selective survival at sea? Are emigrating steelhead from estuarine and upstream habitats different sizes upon ocean entry? Do juvenile steelhead experience differential growth between upstream and estuarine habitats? and Do estuarine reared steelhead have a disproportionately higher ocean survival than those from exclusively upstream habitats?* To investigate these questions, I have quantified the size distribution and abundance of downstream migrants and estuary-reared juvenile steelhead. I compared those data to the juvenile

characteristics of surviving adults using scale morphologies to determine what contribution estuary-reared steelhead made to the adult population. In addition, I used passive integrated transponder (PIT) tags to monitor juvenile-to-adult survival rates of individuals from both estuarine and upstream habitats.

METHODS

Study System:

Scott Creek is a small coastal California watershed draining approximately 75km². It empties into the Pacific Ocean 80km south of San Francisco (37° 02' 28" N and 122° 13' 50" W) (Figure 1). Large waterfalls form impassable barriers on each of the main tributaries, thereby restricting access by anadromous fish to just 23 km of stream. Flow in Scott Creek is highly variable with peak winter flows reaching 28 m³ s⁻¹ (Hayes, unpublished data). Summer and autumn flows, however, may be reduced to 0.08 m³ s⁻¹ during an average year, and during extreme droughts the stream may run dry in the lower reaches. Substratum throughout the watershed is mudstone cobble with the exception of the Big Creek tributary, which is partially granitic cobble. The upper portion of the watershed is comprised of a high gradient stream dominated by a thick coastal redwood (*Sequoia sempervirens*) canopy. The lower gradient main stem of the creek has a lower density overstory cover primarily produced by alders (*Alnus sp.*), with understory dominated by willows (*Salix sp.*). An area of low-lying stream near the ocean forms a small estuary, which is subject to periods of high salinity during large tidal and swell events. The estuary is surrounded by a bullrush (*Scirpus californicus*) marsh. Like many coastal California streams, a

sandbar forms each summer or fall, which causes the estuary to become a freshwater lagoon with infrequent saltwater input from ocean surges.

Native fishes of Scott Creek include steelhead, coho salmon (*Oncorhynchus kisutch*), threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), coastrange sculpin (*Cottus aleuticus*), and tidewater goby (*Eucyclogobius newberryi*). Juvenile starry flounder (*Platichthys stellatus*), and Pacific staghorn sculpin (*Leptocottus armatus*) are infrequently observed in the estuary. A small conservation hatchery has been operated continuously on Scott Creek since 1982, spawning a small number of steelhead and coho salmon each spring that are at least one generation removed from the hatchery (Hayes et al. 2004). Like many southern populations, steelhead in Scott Creek are listed as threatened by the ESA because of low population numbers, despite a relatively unaltered watershed.

Species:

Steelhead, *Oncorhynchus mykiss*, also known as the sea-run rainbow trout, is an anadromous fish endemic to much of the western coast of North America. Although it shares the *Oncorhynchus* genus with seven species of Pacific salmon, all salmon are semelparous, whereas steelhead have the potential to be iteroparous and will return to the ocean after spawning if possible. Like salmon, steelhead have the ability to move between fresh and saltwater through a series of physiological changes that alter the function of their osmoregulatory system. Adult steelhead in central California return from the ocean and begin entering the stream in the winter, following the first freshet (usually late December or early January), with the numbers

of returning adults peaking in February or March, and continuing through late April (Shapovalov and Taft 1954; Hayes et al. 2004). Adults spawn in loose gravel in the main stem and tributaries, and superimposition of redds (nests) may occur as preferred spawning habitat is used multiple times. Egg development time depends on water temperature, but juveniles are generally observed emerging from the gravel four to six weeks after spawning (Shapovalov and Taft 1954) (Figure 2). Upon emergence, juveniles begin exogenous feeding and may remain in the stream from one to four years as parr before beginning the downstream migration (Shapovalov and Taft 1954). Downstream migration of juvenile steelhead begins in the late winter and early spring as a response to lengthening days triggers some parr to undergo physiological, morphological and behavioral changes in preparation for ocean life, thus becoming smolts (Zaugg and Wagner 1973; Hoar 1976; Handeland and Stefansson 2001). The seaward migration of smolts generally peaks in late April or May. During migration, smolts encounter estuarine water just prior to ocean entry, and some percentage of the migrants remain in that habitat. Fish remaining in the estuary may continue to occupy that habitat for an additional 6-9 months before entering the ocean. Steelhead generally remain at sea for 1-2 years before returning to spawn, although a small percentage of spawners have spent three years in the ocean. It is generally unknown what ocean habitats are utilized by central California steelhead, but through limited ocean captures it is safe to assume that at least some adults move far offshore during their ocean migration (Burgner et al. 1992).

Methods Overview

To effectively demonstrate what influence the estuary has on the survival rate of steelhead at sea, it is important to sample both the juvenile and adult populations. Initially, I measured the strength of size-dependent ocean survival with a population of marked hatchery-reared smolts. Then, I monitored growth rates of wild fish in both upstream and estuary waters to examine the potential benefits of each habitat type. Additionally, I evaluated the abundance and size distribution of downstream migrating juveniles (smolts), and those fish that remained in the estuary area throughout the summer and fall. Some of the wild individuals were tagged for later identification to measure individual growth and survival rates. Finally, scale samples were taken from returning adults to identify the size at initial ocean entry and classify the juvenile rearing habitat (i.e., upstream or estuary) through scale morphology.

Estimation of the strength of size selective mortality at sea

In order to determine whether processes of size-selective ocean survival could be driving differential return rates of estuarine and upstream reared fish, I utilized a population of hatchery smolts released in the spring of 2003. I measured the fork length (FL) of 562 hatchery-raised smolts from a pool of 6880 individuals, one week prior to release from the hatchery. Hatchery fish in Scott Creek enter the ocean soon after release (Hayes et al. 2004), therefore I assume that the size distribution of hatchery fish prior to release closely resembled the distribution that entered the ocean. All fish released from the hatchery were adipose fin clipped to permanently mark

their origin as hatchery-reared. Hatchery fish from the 2003 cohort that returned from the ocean as adults in the winter and spring of 2004 and 2005 as 1-and 2-year ocean fish were sampled to determine the size at ocean entry of surviving adults, and the extent of size-dependent survival. Initial size at ocean entry was back-calculated from scale samples using a method described below. The size at release of hatchery smolts was compared to the size at ocean entry of returning hatchery adults with a two-sample T-test to determine whether processes of size-dependent ocean survival were having a strong effect on the resulting adult population.

Sampling of Returning Adult Steelhead

To determine the strength of size-dependent mortality, adults that returned from the ocean in the winter and spring of 2004 and 2005 to spawn were sampled with a floating resistance panel weir, operated daily during the spawning run (Tobin 1994). The weir had a trap box with a one-way door to capture all steelhead moving upstream. The weir operated in stream flows up to $7 \text{ m}^3 \text{ sec}^{-1}$, beyond which the resistance panels fold flat and allow water and debris to flow over the top. Although the successful operation of the weir was flow dependent, 60-80% of the returning adult population were successfully sampled during normal years, as determined by a mark-and-recapture estimate (Hayes, unpublished data). Upon capture each fish was identified as either hatchery or wild origin, measured to the nearest 0.5 cm FL, and weighed to the nearest 0.1 kg. A sample of 10-15 scales was taken from a standard area, just above the lateral line on a diagonal between the posterior attachment of the dorsal fin and the anal fin (Maher and Larkin 1954). All scale samples were

positioned onto waxed weighing paper, which was placed in a labeled envelope and dried for preservation.

Scale Analysis

I used the relationship between fish size and scale size to determine the size at ocean entry of surviving hatchery adult steelhead from the 2003 smolt class. To prepare scale samples for analysis, each wax paper containing dried scales was removed from its envelope and placed under a dissection microscope. All scales were scanned to find the most original, uniform scale available. Original scales (compared to regenerated scales) have complete circuli forming concentric rings from the edge to the core, or focus, of the scale. Scales are also judged for uniformity of shape. Scales that are symmetrical and not overly oblique are preferred for analysis. Up to six of the most original and uniform scales were placed on slides, and flattened with a cover slip. Cover slips were fixed into place with transparent tape. Scales that were original and uniform, but too dirty to be accurately read, were placed into 1ml microcentrifuge tubes with de-ionized water. The tubes were then floated in an ultrasonic bath for 5 minutes at 37° C. Upon removal from the tubes, clean scales were dried on Kim-Wipes[®], and quickly flattened on the slide with a cover slip and allowed to dry flat. Scales were photographed using a microscope mounted Nikon[®] digital camera (DXM1200 3840 x 3072 pixels). The most original, uniform scale from each slide was photographed and saved as an uncompressed TIFF file.

Once each scale had been photographed, OPTIMAS[®] software (Media Cybernetics, Inc., Silver Spring, MD) and a custom macro were used to analyze for: total scale radius (SR, the distance from the focus to the edge of the scale), radius at ocean entry (OER, the distance from the focus to the ocean entry check), number and spacing of each freshwater and ocean circulus, and number of ocean annuli (Figure 3). For ease of reading, all measurements were made 20° off of the longest axis. A qualitative score for each analysis was noted on a scale of 1-3, with a score of 1 being a very original, normally shaped scale with a high reading confidence. Only scales with a score of 1 or 2 were used in further analyses.

There is a strong relationship between fish size and scale size, therefore fish size can be back-calculated from scale size (Ricker 1992). The FL at initial ocean entry was back-calculated on scales from adult steelhead using a regression of FL on SR. The regression was created with original scales from 1251 juvenile and adult steelhead representing the complete range of sizes available. The relationship between SR and FL (Figure 4) is described by:

$$\begin{aligned} \text{(Eqn. 1)} \quad & \text{FL (mm)} = 0.1686 \text{ SR (microns)} + 34.872 \\ & \text{(R}^2\text{=0.97)} \end{aligned}$$

An intercept of 34 mm agrees with other published values of FL at initial scale formation for *O. mykiss* (Snyder 1938; Kesner and Barnhart 1972; Hoplain 1998).

There is some discussion in the literature as to the most appropriate method for back-

calculation of size (Francis 1990; Panfili and Troadec 2002). However, the Fraser-Lee method is widely used, and recent studies have empirically demonstrated its reliability in several fish species, including *O. mykiss* (Davies and Sloane 1986; Klumb et al. 1999). I employed the Fraser-Lee method (Fraser 1916; Lee 1920) in all back-calculations using the formula:

$$(Eqn. 2) \quad L_{oe} = ((L_c - c)(R_{oe}/R_c) + c)$$

where

L_{oe} = fork length at ocean entry of juvenile in mm

R_{oe} = Scale radius at ocean entry of juvenile in microns

L_c = fork length of adult at capture in mm

R_c = Scale radius of adult at capture in microns

c = intercept from (FL) on scale radius (SR) regression (Eqn. 1)

Size at ocean entry of upstream and estuarine reared juveniles

To determine whether juvenile steelhead from both upstream habitats and the estuary entered the ocean at different sizes and numbers, I trapped spring downstream migrants (smolts) each winter and spring (Jan.-June) and sampled the estuary population each fall (Oct.-Dec.). To determine both the number and size of downstream migrants, I placed a fyke net across the stream approximately 50m upstream of the estuary (Figure 1). The fyke net consists of a series of 91cm diameter steel hoops, covered in 6.4 mm (1/4") nylon mesh that are separated by mesh cones

that allowed fish to enter but prohibit their escape. The net has two 1.2m tall seine type wings, which were affixed in the stream to produce a “V” shape and help collect downstream-moving fish in the net. The net was generally run three days per week; however, storm events periodically prohibited the net from being operated. To estimate the number of downstream migrants (N_m), I first calculated net efficiency (E) by releasing a known number of hatchery fish, which are assumed to move rapidly toward the ocean (Hayes et al. 2004) upstream of the net, and count the number captured (Table 2). Net efficiency was estimated as the percentage of hatchery fish caught, and used to estimate the number of wild downstream migrants with the following equation:

$$\text{(Eqn 3)} \quad N_m = (C_m * 365) / E$$

Where

N_m = Estimated number of downstream migrants

C_m = Mean daily catch

E = Trap efficiency (Number of hatchery fish caught/number of hatchery released)

Steelhead captured in the fyke net were placed in aerated buckets until sampling was complete. Each fish was measured to the nearest mm FL, and mass was measured to the nearest 0.01 gram. A sample of 10-15 scales was taken by running the blade of a pair of scissors in the posterior to anterior direction lightly along the side of the fish. Scales were routinely taken from the left side of each fish, but if there was damage to that area scales would be taken from the opposing side. All scales

were placed on waxed weighing paper and dried for later analysis. Finally, each fish ≥ 65 mm FL was scanned for a Passive Integrated Transponder (PIT) tag, using a handheld tag reader (Allflex USA, Dallas Fort Worth Airport, TX.). If no tag was found, then one would be injected using a sterile 12 gauge needle. PIT tags carry a unique identification code so that each fish can be identified later for measurements of individual growth and survival. After sampling, fish were returned to an aerated black bucket to recover for a minimum of 10 minutes before release into the stream. All data was recorded on a Palm[®] handheld computer in the field, and was uploaded to a Microsoft Access[®] database daily.

The estuary habitat was sampled each summer and fall to determine both the population size and the size distribution of estuary juveniles just prior to ocean entry. The estuary habitat, which I define as the area from the beach at the mouth of Scott Creek to approximately 800 m upstream (Figure 1), was sampled monthly using a modified 30 m x 2 m nylon beach seine. A large 2 m x 2 m, 6.4 mm ($\frac{1}{4}$ ") mesh bag was sewn into the center of the seine to help collect fish in the deeper portions of the estuary where pulling the net onto land was not possible. The entire estuary was seined as thoroughly as possible in 50 m sections each month, with the exception of the upper 200 m. Extremely dense plant cover dominated the upper estuary and seining was impossible. All fish were placed into mesh containers in the estuary until all seining was complete, so that fish could not be collected twice. Estuary steelhead were sampled using the same protocol as trap captured downstream migrants.

However, the estimation of size at ocean entry required adjusting the size distribution of the last sampling each fall to account for growth occurring between the last sampling and sandbar breakage. To do this, growth rates from the last sampling event (see: Differential growth of estuary and upstream fish, below), and the number of days between the last sampling and bar breakage were calculated and added to the final fall size distribution. Because the size distributions of spring downstream migrants and estuary fish could not be compared statistically between years due to the change in sampling technique and varying trap effectiveness, all fish were grouped into only two distributions; spring downstream migrants, and fall estuary fish. These two distributions were compared with a two-sample T-test.

To estimate the population size in the estuary each fall, PIT tags were employed in a simple mark and recapture using the Petersen method (Roff 1973). After sandbar closure, I tagged a subset of the fish caught in the newly formed lagoon. In the month following the initial tagging, a new seining effort was performed to assess the number of tagged individuals present and estimate the population size. This process was repeated every month until winter rains made seining of the estuary impossible. The following equations were employed to estimate the estuary population size and variance:

$$\text{(Eqn 4)} \quad N_e = C_e M_e / R_e$$

$$\text{(Eqn 5)} \quad V(N_e) = (M_e^2 C_e (C_e - R_e)) / R_e^3$$

Where

N_e = Estimated estuary population size

M_e = Number of individuals marked in the first seining

C_e = Number of individuals captured in the 2nd seining

R_e = Number of individuals from the 2nd seining that are marked

$V(N_e)$ = Variance of population estimate

Because there are few predators of steelhead in the estuary, mortality is assumed to be negligible in the time between the first and second seining efforts. A mark and recapture was not conducted prior to sandbar closure because of the possibility of individuals entering the ocean and leaving the population during that time. In addition, the number of downstream migrants entering the estuary drops rapidly after June, and I assumed new input to be negligible (Hayes et al. 2004).

In addition to determining the number of fish from the upstream and estuary habitats, it is important to determine how both size class, and date of estuary entry affect the resulting estuary population. To do this, I compared the size distribution of all downstream migrants with the size distribution at downstream migration of those PIT tagged individuals that stayed in the estuary after sand bar closure. Data were organized into 15 mm FL bins from 85 mm to 145 mm, with all fish greater than 145 mm being grouped into the last bin of >145 mm, and a Chi-squared test was used to compare the two distributions.

Sandbar closure often occurs in midsummer, late July or early August during years with normal rainfall. However, downstream migration of juvenile steelhead is

usually complete by early July. The individuals that remain in the estuary throughout the summer are therefore not simply fish that began their migration too late, and were forced to remain in the estuary until sandbar breakage in the winter. To determine what effect timing of downstream migration had in determining what individuals remained in the estuary after sand bar closure, I compared the number of fish per day captured at the downstream migrant trap to the initial capture date for those PIT tagged individuals that remained in the estuary. The two resulting frequency-date distributions were compared with a two-sample T-test.

Differential growth between estuary and upstream habitats

To determine whether differential growth rates between the estuary and upstream habitats may be driving differences in size at emigration for the two populations I sampled fish in each habitat monthly. Upper watershed samples were collected at six sites in the upper watershed that were characteristic of the area and where juvenile steelhead were abundant (Figure 1). All sites were pool habitats that could be sampled effectively during low summer and fall stream flows, and are collectively referred to as upstream habitat, with no distinction between any of the sites. Fish were collected using a 3.2 mm ($\frac{1}{8}$ ") mesh, 4 m x 1 m seine net, or hook and line. For both methods, all collected fish were placed in aerated buckets with fresh stream water until processing, and were sampled with identical methods to downstream migrants and estuary residents.

During regular monthly juvenile sampling at each of the six upstream sites and the estuary, all fish were scanned for PIT tags as an indication of previous

handling. Fish with PIT tags were measured, and specific individual growth rates were calculated using the following equation:

$$\text{(Eqn. 6)} \quad \text{SPGR} = 100 \times [\ln(L_2 / L_1)] / (D_2 - D_1)$$

where

L_1 = FL at initial capture in mm

L_2 = FL at next successive capture in mm

D_1 = date of initial capture

D_2 = date of next successive capture

SPGR = specific growth rate (% change in FL/day)

A mean date of growth was assigned to each growth rate calculation as the midpoint between two fish measurement dates. Growth rates from fish at all upstream sampling locations were pooled, and mean growth rates for upstream fish and estuary fish were generated for each year. Growth rates for both 2003 and 2004 were grouped for each habitat, and were compared with a two sample T-test to look for differences in growth by habitat.

Finally, I investigated the relationship between mean fish growth and mean population density in the estuary after sandbar closure in 2003-2005 to explain potential differences between growth each year. To do this, I generated a regression of mean annual specific growth rate on mean annual estuary population size for each year from 2003-2005. Because the lagoon created by sandbar closure in the estuary each year is of similar size, I assume population size to be a good proxy for density.

Do estuary reared fish recruit disproportionately to the adult population compared to upstream reared individuals?

Size at ocean entry of returning adults

I used four methods to determine whether estuary fish were returning disproportionately to the returning adult population. In the first, I calculated the size at ocean entry of returning adults and compared that distribution with the sizes at ocean entry of emigrating juveniles. The second method involved the classification of returning adults to either upstream or estuary juvenile rearing habitat using a discriminant function analysis and measures of scale morphology. Additionally, I calculated return rates of adult steelhead that were PIT tagged as juveniles at one of the two habitats to determine relative survival rates for each habitat type. Finally, I analyzed scale microchemistry to determine whether elemental scale composition varied between scale growth in each of the two habitats, and whether that variation could be utilized to classify returning adults to freshwater habitat of origin.

I back-calculated the size at ocean entry of wild returning adult steelhead utilizing the same scale measurement technique that was employed in the calculation of size at ocean entry for returning hatchery fish. Scale samples were collected from 439 wild adults from spring of 2002 through spring of 2005. Although some 1-year ocean fish were captured and assigned to the 2004 ocean entry group, these samples were omitted from this analysis because of the potential bias of using only “early” returning fish to classify the entire 2004 cohort. After removals, 364 original, uniform, scale samples that received a score of 2 or better during reading were used

for the final analysis. Because of the difficulties of identifying freshwater annuli in adult scales, especially in estuary residents, returning adult steelhead were not assigned to a particular downstream migrant cohort for comparison. Instead, all returning adults were grouped together as one class, and compared to grouped estuary fish and downstream migrants from all years. Analysis of variance (ANOVA) was conducted to evaluate the relationship between fish FL and fish type. The independent variable, fish type, had three categories: spring downstream migrant, fall estuary, and FL at ocean entry of returning adults. Fork lengths for each group were data for all sampling years combined. Fork length was the dependent variable.

Scale morphology DFA

In addition to size, I used circuli spacing and spacing variance to distinguish between adults reared as juveniles in the estuary and those reared upstream. Circuli spacing in scales is correlated with growth in both coho (*Oncorhynchus kisutch*) (Fisher and Pearcy 1990; Fisher and Pearcy 2005), and sockeye salmon (*Oncorhynchus nerka*) (Fukuwaka and Kaeriyama 1997), therefore it is reasonable to assume that the relationship holds true for steelhead as well. The origin of fish in mixed stocks of hatchery and wild steelhead has been determined successfully by differences in scale morphology attributable to different growth regimes in the hatchery and the wild (Maher and Larkin 1954; Bernard and Myers 1996; Tattam et al. 2003). To provide an indication of estuary-derived growth, I calculated the mean circuli spacing and variance for the last 18 circuli of juvenile fish of all size classes from the upper watershed and estuary. Although many combinations of circuli were

tested in a stepwise fashion, the mean of the last 18 circuli was most effective at discriminating between prior habitat use, while simultaneously removing problems of non-independence in sampling. Upstream samples were collected throughout the year, but because individuals only use estuary habitat after a prior stay in the upper watershed, estuary samples were taken in the late fall when the estuary growth signature has been maximized. To separate upstream and estuary-reared juveniles, mean circuli spacing and the variance of circuli spacing were used in a discriminant function analysis (DFA). The mean spacing and variance of the last 18 freshwater circuli of scales from returning adults were then included in the DFA to classify the freshwater life-history path returning adults had utilized as juveniles.

Ocean survival of PIT tagged juveniles

In order to calculate the ocean survival of juvenile steelhead, I placed PIT tags in 640 steelhead at both the downstream migrant trap and the estuary in the spring and summer of 2003. Through mark and recapture, I was able to estimate the number of tagged fish that remained in the estuary after sandbar closure. Some returning adults in the winter and spring 2005 were carrying PIT tags from the 2003 deployment (Adults returning in 2004 were checked, but no tags were found.). I used estimates of the number of juvenile PIT tagged fish from each habitat, and the number of returning adults from each habitat to calculate the survival rate of fish from each habitat. In addition, scale morphology was analyzed for each returning adult to determine whether the number of ocean years expressed on each scale matched with

expected time of ocean entry based on measured juvenile habitat use from PIT tag recaptures.

Scale microchemistry

In addition to patterns of morphology, I explored scale microchemistry to identify periods of estuary residence. Because fish live in an aqueous environment, they obtain the raw materials for growth from both their diet, and the surrounding water. As calcified tissues are formed, fish incorporate many elements present in the water in the proportion they are found in the environment. It is fortuitous that the abundance of these elements varies in different water masses. Scales, comprised of a calcium phosphate matrix, have successfully been used as a historical record of habitat use where water chemistry varies between discreet regions (Wells et al. 2003).

To test whether estuarine residence was recorded in scales as an area of mixing between fresh and oceanic water, I used scales collected from juvenile steelhead that were sampled just prior to their entrance into the estuary and compared these to scales collected from the same individuals after at least one month of estuarine residence. Scales were cleaned under a laminar flow hood by placing them in a microcentrifuge tube with 2mL of Millipore[®] Milli-Q ultrapure water. The microcentrifuge tubes were placed in an ultrasonic bath for 10 minutes to remove any surface material. Scales were removed from the microcentrifuge tubes and placed in a second, empty tube to dry. Dried scales were then mounted on petrographic slides with double sided tape (3M[®] 665 permanent-linerless double coated tape). Scale chemistry was analyzed with a VG Excel quadrupole inductively-coupled plasma

mass spectrometer (ICP-MS) coupled with a 193 nm Excimer laser. Scales were pre-ablated with the laser to remove any possible surface contamination by running a laser transect from the focus to the edge along the same 20° offset that was used to measure scale morphology (travel rate: 60µm sec⁻¹, spot size: 70µm, firing rate: 1Hz). The scale sample was collected for introduction to the ICP-MS immediately following pre-ablation by running a second transect along the original transect (travel rate: 5µm sec⁻¹, spot size: 10µm, firing rate: 10Hz). Thirteen elements were targeted for analysis with the ICP-MS: ⁷Li, ²⁴Mg, ⁴³Ca, ⁵⁵Mn, ⁶⁵Cu, ⁶⁶Zn, ⁸⁸Sr, ¹³⁷Ba, ¹³⁸Ba, ¹³⁹La, ¹⁴⁰Ce, ²⁰⁸Pb, ²³⁸U. Data were binned to generate a mean value for each five micron interval, and each element was converted to an elemental ratio with respect to calcium to account for differences in the amount of material introduced into the ICP-MS. Transects from multiple scales taken from the same individuals over time were compared to ascertain how stable the chemical signal of each habitat was, and whether those signals were strong enough to identify juvenile habitat use in returning adult steelhead.

RESULTS

Estimation of the strength of size selective mortality at sea

Hatchery smolts released in April of 2003 encountered strong size selective mortality at sea. Smolts measured just prior to release had a mean FL of 158 mm (SD=35). Few hatchery fish were observed in the stream two weeks after the release date, and hatchery fish were not found to use the estuary habitat (Hayes et al. 2004)

Original scales were obtained from hatchery fish returning as adults in the winter/spring of 2004 and 2005 as 1-and 2-ocean year fish, respectively. Back-calculation of FL at ocean entry indicated that the surviving adult population had a mean FL at ocean entry of 181.2 mm (SD=28.9), which was significantly larger upon ocean entry than the initial population of fish released from the hatchery ($t(592)=4.47$ $p<0.001$, Figure 5).

Size at ocean entry of upstream and estuarine reared juveniles

The mean FL of downstream migrating smolts in 2002 and 2003 was 110 mm. The mean FL of 2004 downstream migrants was 92 mm, however, net mesh size was changed from 9.5 mm ($\frac{3}{8}$ "") to 6.4 mm ($\frac{1}{4}$ "") and the net became more effective at catching the smaller individuals that were not sampled in 2002 and 2003.

Additionally, high flows in the spring of 2005 prevented net operation until late in the season, and early migrants were not sampled. Because of these discrepancies in sampling, I did not compare downstream migrant size distributions between years.

The total number of downstream migrating steelhead is estimated for 2003 and 2004 (Table 1). No population size is estimated for 2002 or 2005 because of the lack of early season samples due to excessive stream flow.

The size distribution of the estuary population upon bar breakage each winter varied by year, mean FL upon winter sandbar breakage was largest in 2003 at 213 mm (SD=32), and smallest in 2004 at 182 mm (SD=26), but estuary fish from all years (2002-2005) were significantly larger than spring downstream migrating juveniles in the same years ($t(455.4)=45.76$ $p<0.001$, Table 2). The estuary

population varied by year, but was between 8 (2004) and 48 (2003) percent of the downstream migrant population where estuary mortality is assumed to be low (Table 1).

Stay in estuary or go to sea?

Of the 298 fish I measured and PIT tagged at the downstream migrant trap in spring of 2003, 61 fish were recaptured in the estuary after sandbar formation in the fall. The initial FL at estuary entry was compared between the two groups of fish to determine what sizes of fish remained in the estuary. A Chi-Square test was used to compare the two distributions and a significant difference was found, indicating that the initial size of downstream migrants was larger than the initial size of those individuals that remained in the estuary $\chi^2(5, N=359)=15.36$ $p=0.009$. No fish with an initial estuary entry FL larger than 150 mm was observed after sandbar closure, indicating that those fish move to the ocean before bar formation (Figure 6). The mean downstream trap tagging date for all tagged fish and those that stayed in the estuary was not significantly different ($t(227)=0.490$, $p=0.625$) indicating that the timing of downstream migration did not have an effect on the resulting downstream migrant population, and fish from throughout the entire run inhabited the estuary after sandbar closure.

Differential Growth Between Estuary and Upstream Habitats

Specific growth in the estuary was significantly greater than upstream habitats for 2003 and 2004 ($t(501)=22.7$, $p<0.001$, Figure 7). Mean growth in the estuary for 2003 and 2004 was 0.36% increase in FL per day, while mean upstream growth was

0.06% increase in FL per day for the same period. A strong negative relationship between growth rate and population size among the three years sampled ($R^2=0.99$), suggests that estuary growth rate among years is at least partially explained by differences in steelhead density among years (Figure 8).

Do estuary reared fish recruit disproportionately to the adult population compared to upstream reared individuals?

Size at ocean entry

To determine whether returning adults were recruiting disproportionately from one of the two general habitats, I compared the size at ocean entry of the two juvenile groups from 2002-2005 with the size at ocean entry of returning adults from the same years (Figure 9). For all sampling years combined, FL at ocean entry differed significantly among the spring downstream migrants, fall estuary residents, and back-calculated returning adults (ANOVA: $F(2, 1802)=2192.9$, $p<0.001$). Post-hoc comparisons using the Tukey test indicated that there were significant differences among all three groups. However, the mean FL of spring downstream moving smolts for all years was 106 mm (SD=26, n=1108), while fall estuary fish was 198 mm (SD=33, n=331), and ocean entry FL of returning adults was 208 mm (SD=38, n=364).

Habitat Classification by Circuli Spacing

In order to provide another independent measure of juvenile freshwater rearing habitat of returning adult steelhead, I used measures of scale spacing as a proxy for juvenile growth, with large spacing indicating faster growth and estuary

residence, and smaller spacing indicating lower growth and upstream residence. Mean circuli spacing of the last 18 circuli of scales from estuary (n=96) and upstream juveniles (n=92) were log transformed. Spacing was significantly different between upstream and estuary fish ($t(186)=13.95$ $p<0.001$, Figure 10). A discriminant function analysis (DFA) using mean spacing and variance of spacing of the last 18 freshwater circuli as predictors was performed to assign juveniles to their respective rearing habitat. The DFA jackknifed classification indicated an 86% correct assignment (83% for estuary, 90% for upstream) to either habitat. Scales from all adult fish with a reading score of two or better (n=406) were analyzed to determine the mean spacing and variance for the last 18 circuli prior to ocean entry. Spacing was significantly wider than either the estuary or upstream individuals $F(2, 593)=151.8$, $p<0.001$, Tukey post-hoc test. The DFA was then used to assign returning adult steelhead to one of the two juvenile rearing habitats (Upstream or Estuary) based upon the same parameters used to in the juvenile habitat assignment (mean spacing of the last 18 circuli, variance of spacing). Of the 406 adults analyzed, the DFA jackknifed classification matrix assigned 61 ± 9 (15%) returning adults to upstream juvenile habitat, while 344 ± 48 (85%) were assigned to estuary juvenile rearing habitat.

Pit Tag Recaptures and Survival

I estimated through mark and recapture that 1 in 10 steelhead in the estuary was carrying a PIT tag by December of 2003. In winter and spring of 2005, 142 returning adult steelhead were sampled. Thirteen adults (7 males, 6 females) were carrying PIT tags implanted when they were juveniles. All 13 individuals were

observed in the estuary in 2003. Scale analysis indicated that all of the tag-carrying adults had only one year of growth in the ocean, indicating that they had not entered the ocean until spring of 2004. In addition, the PIT tagged adults maintained nearly the same tag ratio (1:10.9) in the returning adult population that I observed in the estuary in 2003, indicating that it is probable that many of the returning adults not carrying tags were also products of the estuary juvenile rearing environment.

Ocean survival of all Scott Creek steelhead from 2003 was estimated from the percentage of PIT tag recaptures from adults captured in winter of 2005 and 2006 (no 2003 tagged steelhead were captured in 2004). Thirteen tags were recovered in 2005, however, only 78% of returning steelhead were sampled (Hayes, unpublished data), which indicates that approximately 17 tagged steelhead returned that year. In addition, 4 tags were recovered in 2006, however, since the 2006 adult return season has not yet ended, there is no sampling efficiency currently available for 2006. A total of 640 juveniles were tagged at both the downstream migrant trap and the estuary in 2003, which indicates a population-wide smolt-to-adult survival rate of at least 3.3%. However, all tags recovered were from estuary-reared fish, as revealed by tagging histories and scale analysis. I estimate that there were 254 tagged fish utilizing the estuary habitat in the fall of 2003 from the population size (2540) and the ratio of tagged to untagged fish (1:10). This indicates an 8.3% survival of the estuary-reared population.

Scale Microchemistry

Ratios of each element or isotope to calcium along scale focus-to-margin transects were plotted for each fish to compare before and after estuarine growth samples. Most elements showed no significant change in ratio upon estuary entrance. However, the Mn:Ca and $^{138}\text{Ba}:\text{Ca}$ ratios showed changes in their elemental ratios after estuary entrance (Figure 11). Unfortunately, these data also indicate that there is only partial stability between the samples, and previous signatures had been altered in the time between when each sample was taken. Given the short time between the first and second scale samples from each individual and the relative instability of chemical content, I can conclude that the chemical composition is likely not stable enough to retain signatures of estuary residence throughout the entire ocean phase.

DISCUSSION

This study provides evidence for the importance of estuarine habitat to central California steelhead populations. A strong size-dependent ocean survival coupled with a large dichotomy in sizes between estuary and upstream-reared smolts, has led to a large survival advantage for the larger estuary-reared individuals. These patterns are driven by the difference in growth rates between productive estuary waters and the relatively oligotrophic upstream habitat.

Estimation of the strength of size selective mortality at sea

Although evidence of size selective survival is not new (Sogard 1997), the strength of size selective survival coupled with an extreme dichotomy in sizes of

ocean entry between the two general rearing habitats (upstream tributaries and estuary) could lead to size selective survival being the largest determinant in driving which individuals ultimately return to the adult population. Back-calculated size at ocean entry for 2003 hatchery juveniles as adults returning in 2004 and 2005 indicated that small hatchery smolts (≤ 150 mm FL) were underrepresented in the returning adult population, and larger smolts (> 200 mm) were overrepresented. These data support the size-biased survival proposed by Ward and Slaney (1989) for a northern stock of steelhead. Because few hatchery fish were observed in the upper watershed or estuary after planting, I assume that fish of all sizes completed the ocean migration and the resulting ocean-entry size distribution of returning adults was created through size-dependent selection in the marine environment. It has been shown that hatchery-reared salmon may experience lower overall survival in the marine environment (Jonsson et al. 2003). Although this inherent difference in smolt quality could be driving the size-biased survival in the resulting returns, I would argue that although hatchery fish may suffer a lower overall survival, the processes shaping the size distribution of surviving fish (i.e., predation, foraging success) should act similarly on both hatchery and wild populations. This would suggest that wild Scott Creek smolts should also experience a strong size-biased survival.

Size at ocean entry of upstream and estuary reared juveniles

Downstream migration

Spring downstream migrants enter the Scott Creek estuary at a relatively small size compared to smolting steelhead in more northern populations (Ward and Slaney

1988) (Figure 9). This is consistent with the relatively low growth rates observed in upstream habitats of Scott Creek (Hayes et al. 2006, unpubl. data), and what was observed by Shapovalov and Taft (1954) in nearby Waddell Creek. While the estimated number and mean size of downstream migrants differed annually (due to both a change in net mesh size and differences in flow affecting the number of days the net could be operated each year), these differences are minimal and still indicate that the vast majority of Scott Creek steelhead move downstream at a very small size.

Estuary Residence

The estuary population of steelhead is comprised of juveniles that emigrated from the upper watershed in the spring and summer. The largest downstream migrants (>150 mm FL) move through the estuary and are not observed again as juveniles, indicating that they are large enough to move directly to sea without additional growth. It is certainly possible that young steelhead in Scott Creek are migrating at a small size specifically to take advantage of the favorable estuary growth potential. The estuary population each fall varied between 8 and 48% of the estimated total number of downstream migrants (in 2004 and 2003, respectively). However, 48% estuary utilization in 2003 is probably an overestimate, because a large mesh size was used in the downstream migrant trap that year, effectively underestimating the number of downstream migrants. Timing of sandbar formation does appear to impact the overall number of downstream migrants that will reside there. In years when high flow prevents early season sandbar formation, productive deep water is not found until the late summer and may harbor fewer fish. On the other

hand, early sandbar formation during low flow years leads to productive habitat being available during peak downstream migration, and may cause more fish to remain in the estuary throughout the summer.

Differential growth between estuary and upstream habitats

Growth rates in the estuary are extremely high, nearly 10 times what is observed in the upper watershed for some portions of the year (Figure 7). This leads to average downstream migrants doubling their FL with only a few months of estuary residence. High growth is probably due to the abundance of gammarid amphipods (*Gammarus* sp.) in the estuary, which are a preferred food source of steelhead inhabiting coastal estuaries (Needham 1939). Although only qualitative surveys were performed, gammarids were not observed upstream of the lagoon. Incidentally, fall estuary fish were similar in size to smolts found in more northerly populations (Ward and Slaney 1988; Lohr and Bryant 1999). This may indicate that estuaries in central California are filling a role that upstream waters have in the northern part of the steelhead range.

Although growth rates in the estuary were always higher than the upper watershed, growth in the estuary appears to be density-dependent, with growth rates decreasing as the number of fish utilizing the estuary increases. However, the decrease in growth rates with increasing fish density had little effect on the eventual size of fall estuary fish. This is probably due to annual flow regimes altering the number of days that productive lagoon conditions were available to young steelhead. Therefore, during low flow years when deep-water conditions formed earlier, the

population was larger and growth rates were lower, but each fish had a longer period of time to experience that habitat before winter bar breakage allows fish to move to sea. Because of this dynamic, fall estuary fish were very similar in size regardless of sandbar formation date and population size. It is important to note however, that the estuary is currently quite small and the sandbar formation dynamics may be very different since coastal development in the 1930's restricted the Scott Creek estuary to a fraction of its historic size³. In fact, the severe alteration of the estuary is probably the largest anthropogenic change to the watershed, as much of the upper watershed remains in an undeveloped state.

Juvenile steelhead growth in the estuary is relatively unaffected by competition for prey by other fish species. Coho salmon are abundant during some years in Scott Creek, but are rarely observed in the estuary, and do not appear to reside there for more than a few weeks. Threespine sticklebacks are often found in abundance in the estuary, although it is unclear how much competition for resources exists between these species.

It is likely that estuary mortality is low in Scott Creek because there appear to be few predators. Unlike many estuaries, no marine mammals have been observed in the Scott Creek estuary. Prickly sculpin have been observed feeding on smaller steelhead in the upper watershed, however most steelhead entering the estuarine water were probably large enough to avoid predation by prickly sculpin. Avian predators

³ California Highway 1, constructed in the late 1930's along the California coast potentially altered the size and seasonal dynamics of estuaries in many watersheds, Scott Creek included, as indicated by historic aerial photographs.

are an important source of mortality for estuarine salmonids, particularly steelhead in the Columbia River estuary, with birds consuming greater than 10% of the steelhead previously detected moving into the estuary (Ryan et al. 2003). Avian predators, while often present, are found in low numbers in the Scott Creek estuary. To a limited extent mergansers have been observed, but they appear to utilize upstream areas with riparian cover more readily than the open estuary habitat. In fact, the deeper estuarine water may provide a refuge from the avian predators (e.g., mergansers, *Mergus* sp.; kingfishers, *Ceryle alcyon*; great blue herons, *Ardea herodias*) that readily feed on steelhead in the shallower upstream waters. Further study is required to determine what effect predation has on the distribution and density of steelhead in the estuary. It is certainly possible though, that steelhead utilize the Scott Creek estuary specifically because of the excellent growth opportunity it provides, and the relatively low predation pressure compared to marine environments. Additionally, small coastal estuaries in central and southern California streams appear to function much differently than larger estuaries (e.g., Columbia River mouth, San Francisco Bay). Many of the larger estuaries have extensive populations of large piscivorous fish (e.g., cutthroat trout, *Oncorhynchus clarki*; striped bass, *Morone saxatilis*), and potentially vast communities of competitors (e.g., other salmonids, *Oncorhynchus* sp.; perch, Percidae; shad, *Alosa sapidissima*; smelt, Osmeridae; sole, Soleidae) and extended residence in these areas may not offer the same advantages that smaller estuaries, with few other fish species may provide.

Do estuary reared fish recruit disproportionately to the adult population compared to upstream reared individuals

Scale chemistry

Scale microchemistry indicated that there may be compelling trends in the chemical signatures imparted in calcified structures as an indicator of habitat use. However, there appears to be instability issues in the chemical composition of scales, with potential overwriting of previous chemistry (Figure 11). This may be due to the physiological changes associated with smoltification. Fish do have the capacity to draw upon scales when calcium is needed, and chemical signatures may be lost during that process (Persson et al. 1998; Persson et al. 1999; Kacem et al. 2000). In addition, when estuary sandbar formation occurs, the estuary often becomes mostly freshwater, which may be nearly identical in chemistry to the upstream tributaries. What few pockets of salinity remain during this time become hypoxic, reduced environments over time and are easily avoided by inhabiting steelhead. Although chemical analysis of scales indicated some patterns of interest, more work is needed to establish the potential for long-term stability in anadromous fish.

Size at ocean entry

Back-calculation of size at ocean entry from the morphological characteristics of scales from returning adults indicates that surviving adults were quite large as juveniles at ocean entry. In fact, the vast majority of survivors were so large at ocean entry that the upstream waters alone could not have produced them, as indicated by the size of downstream migrants (Figure 9). Only one returning adult had an ocean

entry size (90 mm FL) near the average downstream migrant size (106 mm FL). Fewer than 15% of downstream migrants were above the size threshold (140 mm FL) where the vast majority of returning adults originally went to sea. Additionally, only a small fraction of downstream migrants (<0.01%) captured over 4 years (2002-2005) were larger than 200 mm FL, yet the majority (56%) of returning adults were at least that size upon ocean entry as juveniles. Size-dependent survival in both wild and hatchery fish indicates that small fish are less likely to survive in the marine environment, and estuary-reared juveniles comprise most of the returning adult population.

Scale morphology

Although the relationship between somatic growth and rate of circuli deposition may be somewhat weak, I was able to use the spacing and variance of the spacing to successfully discriminate between estuarine and upstream-reared individuals with 86% accuracy because growth rates are very different in the two habitats. I was then able to assign each returning adult to a freshwater rearing habitat. The vast majority of adult steelhead (~85%) were assigned to rearing in estuary habitat, regardless of their year of return, or year of ocean entry. Habitat assignment by circuli spacing and size at ocean entry give two independent measures of habitat use that both implicate the estuary as having been used by most surviving adult steelhead as juveniles.

PIT tag returns

Some adults returning in the winter and spring of 2004/2005 carried PIT tags from juvenile implantation. Because these fish returned in nearly the same ratio in which estuary fish were tagged (1:10.9 vs. 1:10 respectively) there was probably a large number of untagged estuary-reared fish, which returned as well, which is indicated by the scale circuli spacing data. Because estuary fish were tagged randomly, there is no reason to believe that there was any bias in the return of tagged fish over untagged individuals. Every adult that returned with a PIT tag was either tagged or observed in the estuary during the summer and fall. This is further evidence that migrating steelhead that did not use the estuary experienced very poor survival at sea. I estimated survival rates of estuary-reared juveniles to be 8.3 percent from the 2003 estuary cohort, as compared to the 3.3 percent of the total population from the 2003 cohort. However, no fish tagged at the spring migrant trap that were not observed in the estuary in the summer and fall of 2003 were recaptured as adults, further indicating a weak ocean survival of the 2003 smolt class that did not utilize the estuarine habitat.

CONCLUSIONS

The results of this study support the contention of size-dependent ocean mortality of central California coastal steelhead. Further, these data strongly suggest the estuary as being important nursery habitat for producing large steelhead with increased ocean survival. Estuarine waters in Scott Creek comprise less than 3% of

the habitat available to steelhead, yet the vast majority of the adult population may be products of that environment. This indicates that coastal estuaries may be more important to steelhead persistence in the southern portion of their range than previously thought, and their degradation could have drastic implications for steelhead populations already listed as threatened or endangered. Indeed, restoration of coastal estuaries may be an effective method of returning steelhead to their historic population levels in these watersheds. Finally, more work is needed to determine what strategies steelhead take in watersheds without estuaries, to achieve a size large enough to survive at sea without the additional growth these habitats afford. In addition, the strength of size-selective mortality in the ocean appears to be strong enough that the very small size at ocean entry observed in Scott Creek should not persist in the population. More work is needed to determine what conditions may favor the small size at ocean entry and why it is maintained in the face of strong selection against small smolts.

Table 1. Proportion of downstream migrating juvenile steelhead utilizing the estuary in 2003 and 2004.

Year	# of hatchery fish released	# of hatchery fish captured	Estimated % of hatchery fish captured	# of wild downstream migrants captured	Estimated total # of wild downstream migrants	Estuary population \pm SD	% of downstream migrants utilizing the estuary
2003	7500	827	11.02	581*	5272*	2540 \pm 479.4	48
2004	3770	470	12.46	2287	18354	1489 \pm 381.9	8

* 2003 is assumed to be an underestimate because of the large mesh size of the net used to capture downstream migrants.

Table 2. Mean FL of downstream migrants and late summer estuary residents.

Year	Downstream Migrants			Estuary Residents	
	Trapping Dates	n	Mean Fork Length (mm) ±SD	Estuary Population ±SD	Mean Fork Length at Ocean Entry ± SD
2002	April-July	370	110.2 ±25	N/A	196.2 ±21
2003	Jan.-July	386	110.0 ±29	2540 ±479	213.6 ±32
2004	Jan.-July	306	92.6 ±24	1489 ±381	182.5 ±26
2005	March-July	113	96.0 ±25	540 ±93	191.1 ±33
All Years		1175	102.2 ±26	1523 ±317	195.8 ±28

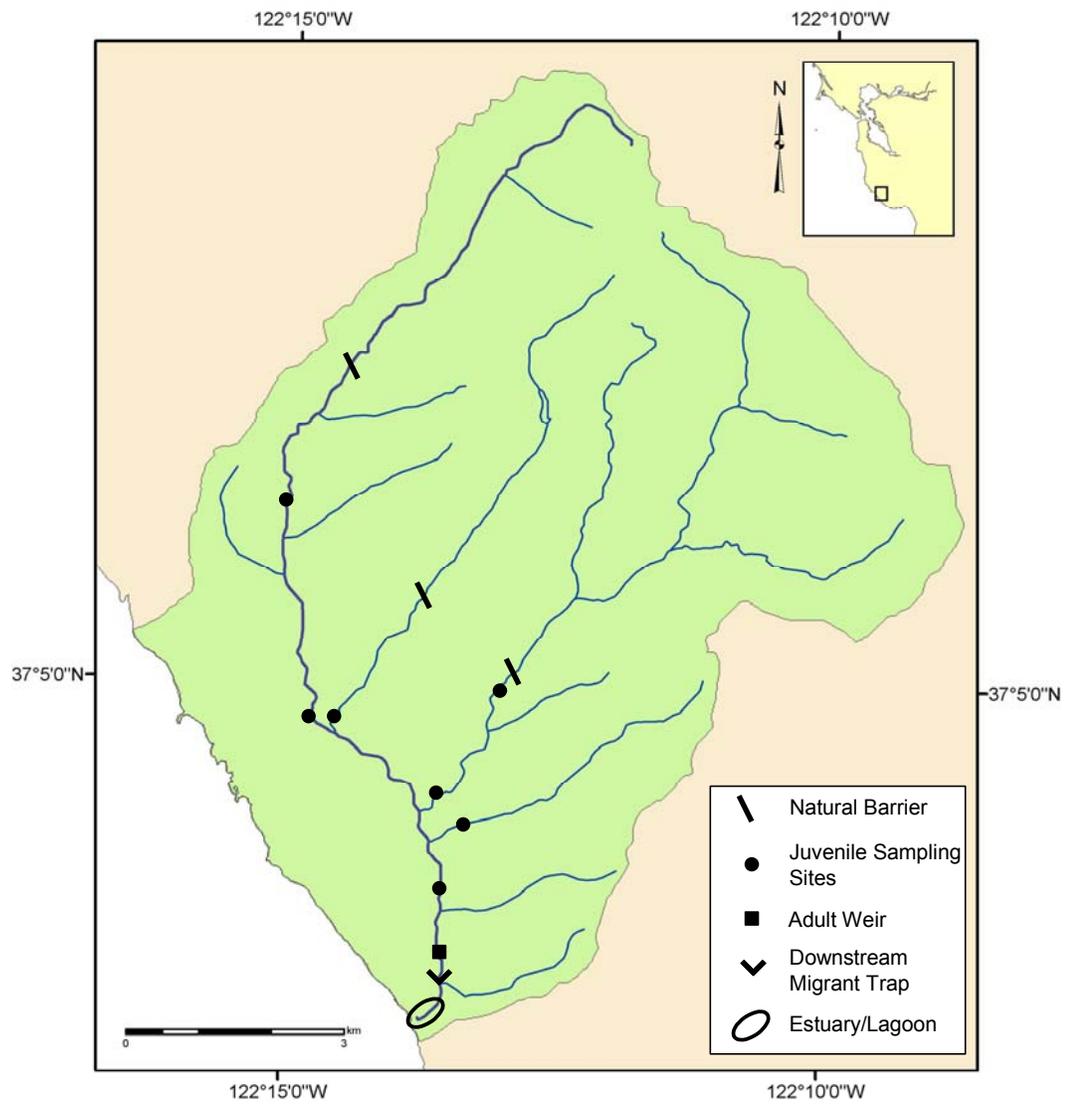


Figure 1. Scott Creek Watershed

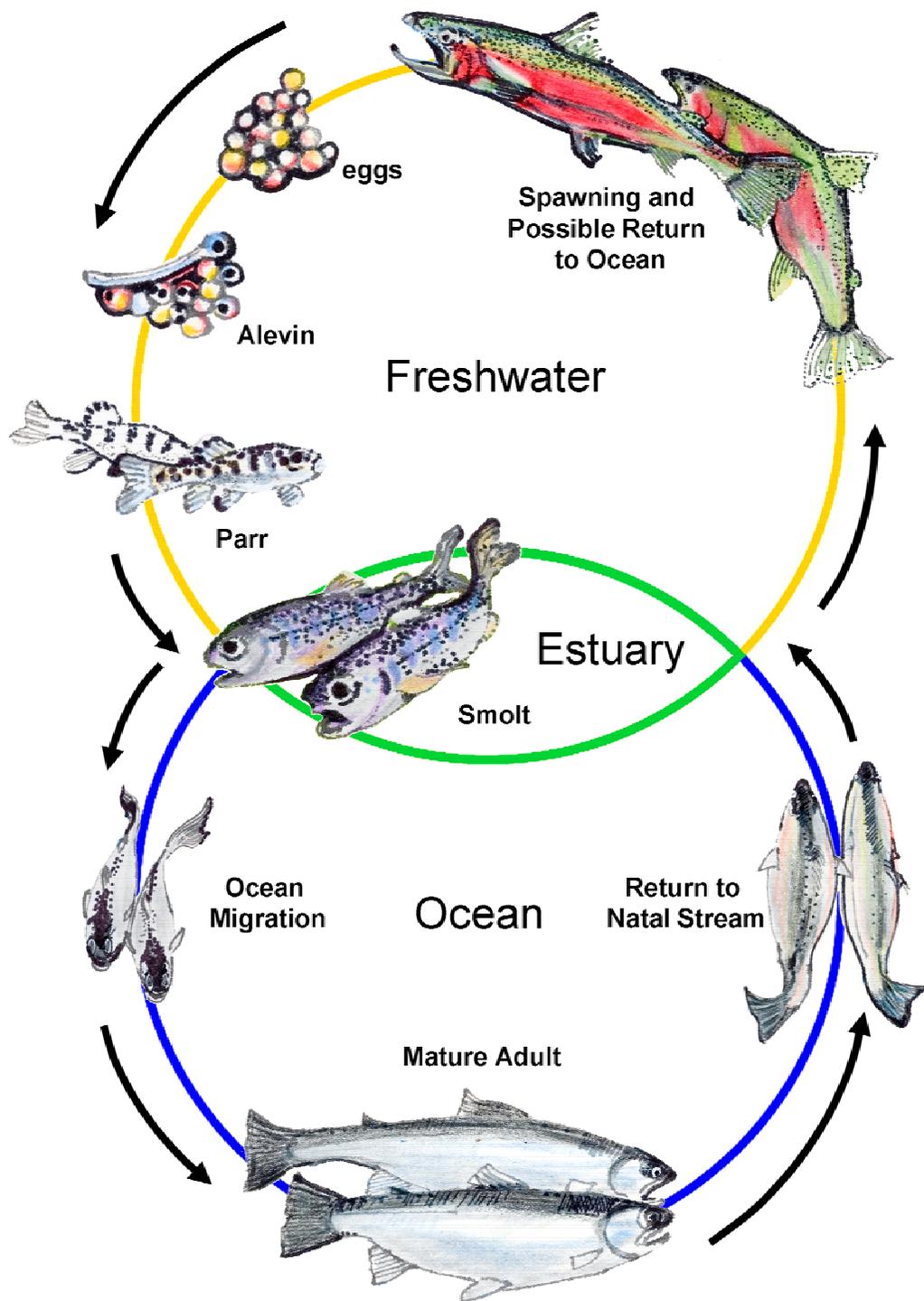


Figure 2. Steelhead Life-Cycle (Drawings by Susan Turner)

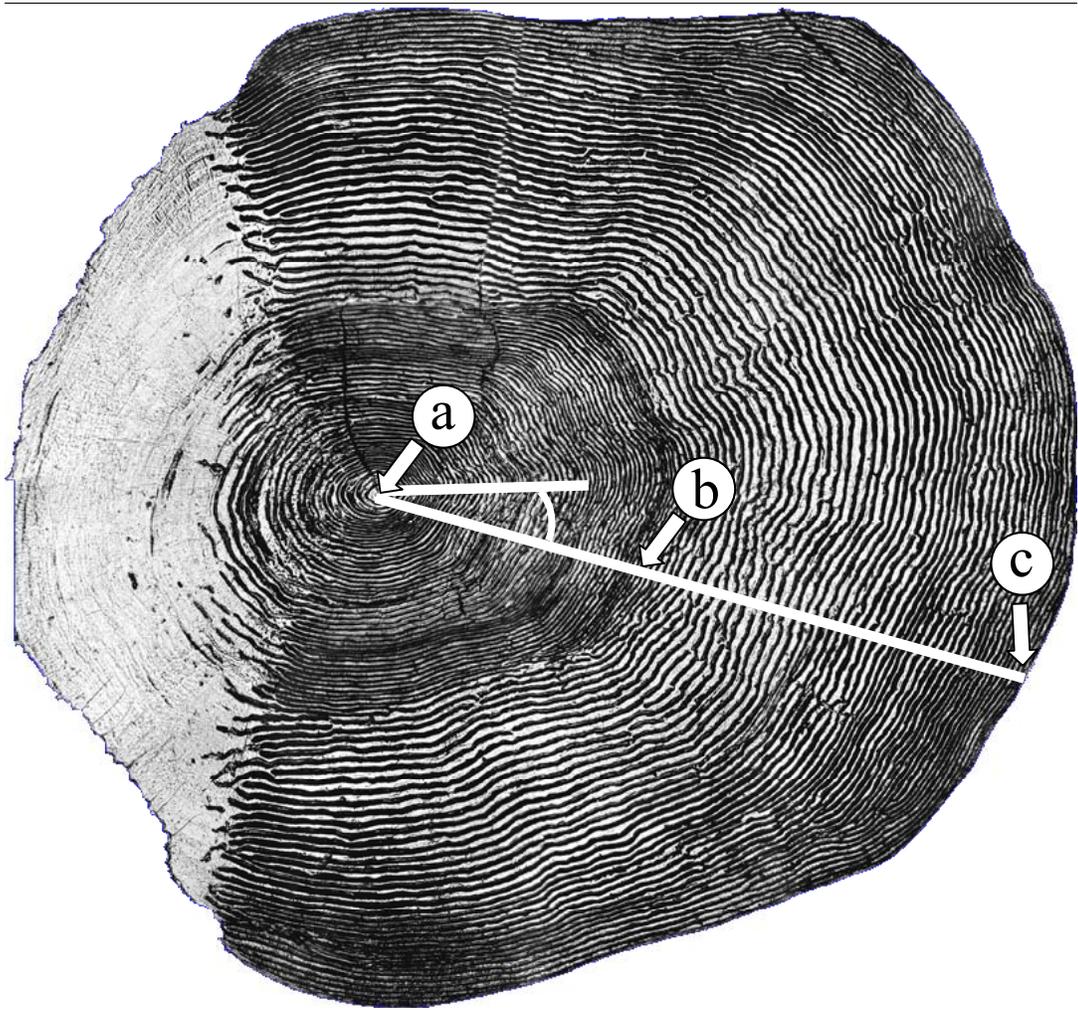


Figure 3. Photograph of scale indicating; a, focus of scale, b, ocean entry radius (OER) and c, scale radius (SR) and the 20° offset from the center axis used to make measurements.

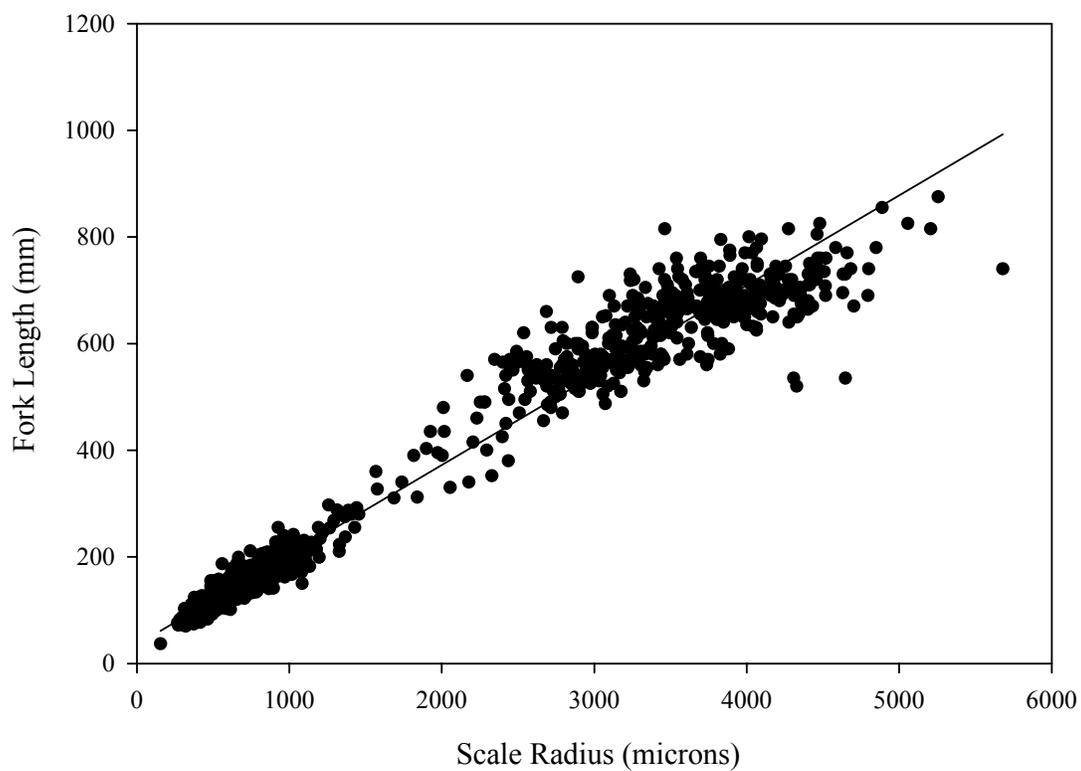


Figure 4. Relationship between fork length and scale radius based on scales from juvenile and adult steelhead collected throughout the watershed n=1250 (2002-2005). $FL=0.1686(SR)+34.87$ $R^2=0.97$

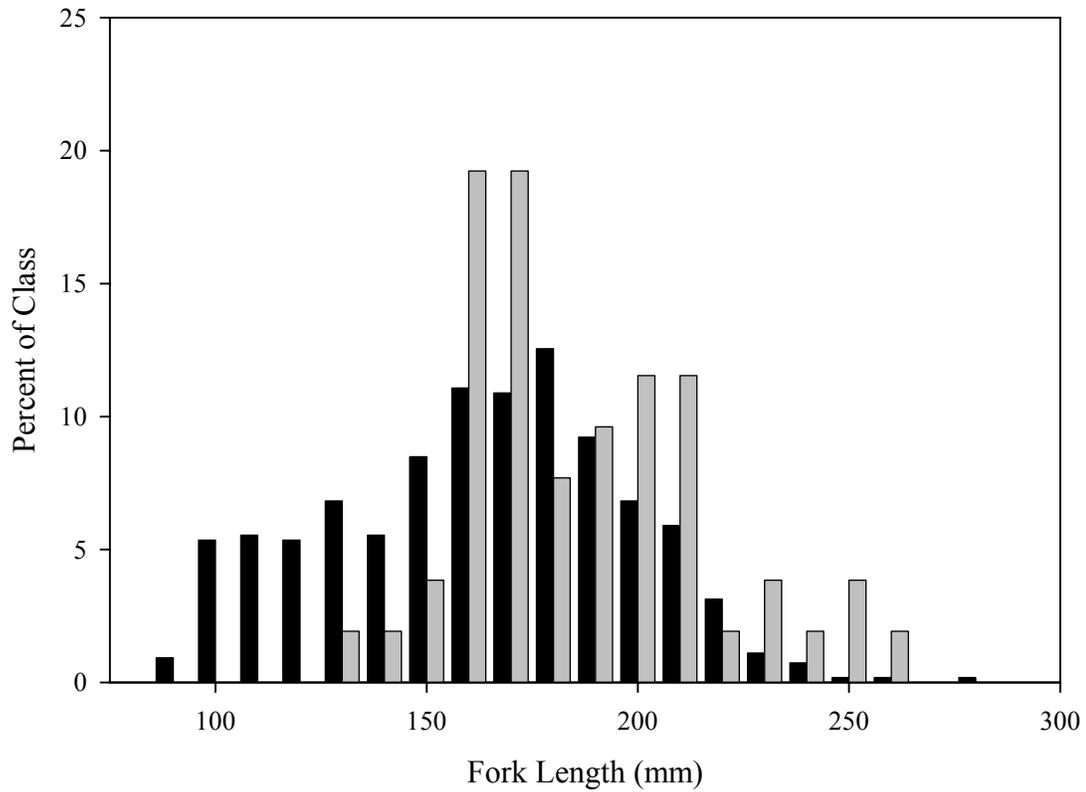


Figure 5. Size distributions of juvenile hatchery smolts (n=542, black bars) sampled immediately preceding release, and the back-calculated size at ocean entry of surviving adults from the same cohort (n=52, grey bars).

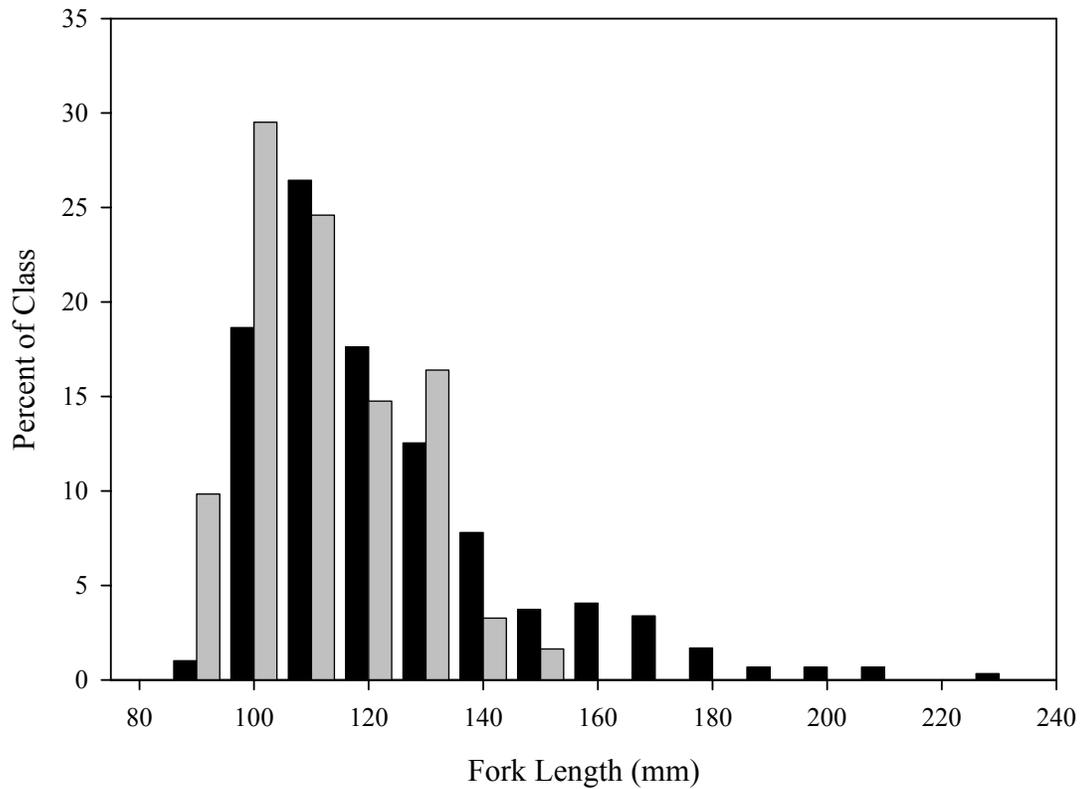


Figure 6. Size distribution of spring downstream migrants PIT tagged prior to estuary entry (n=298, black bars), and the size at initial estuary entry of tagged fish recaptured in the estuary after sandbar closure (n=61, grey bars).

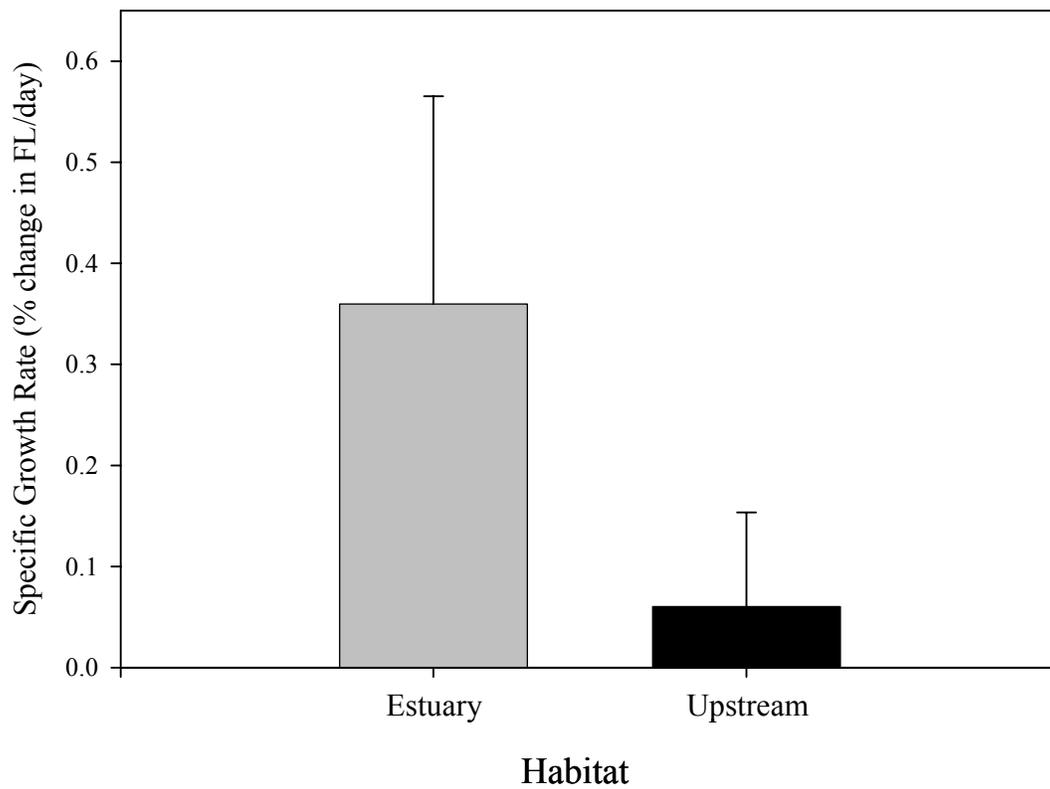


Figure 7. Specific mean (+1 SD) daily growth rates of estuary-reared (grey bar) and upstream (black bar) juvenile steelhead for 2003 and 2004.

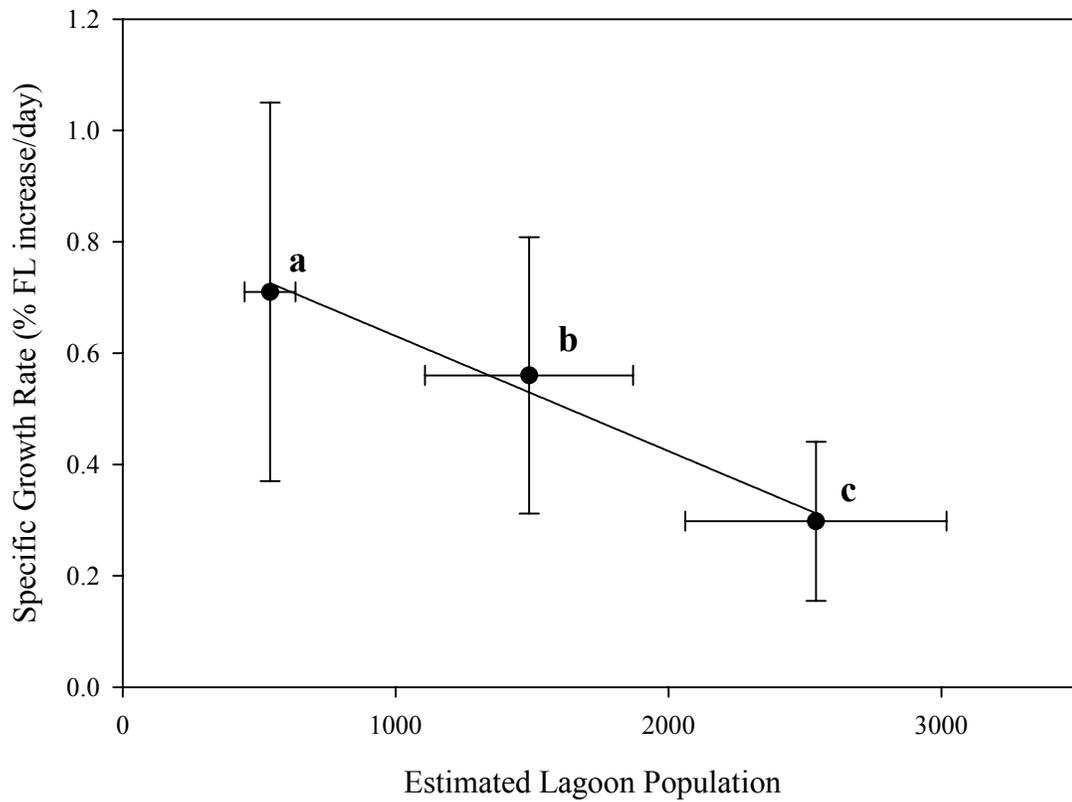


Figure 8. Estimated post-closure estuary population sizes and growth rates from (a) 2005, (b) 2004, (c) 2003. All data are means \pm SD. $SPGR = -0.000206(\text{Population Size}) + 0.837$ $R^2 = 0.98$

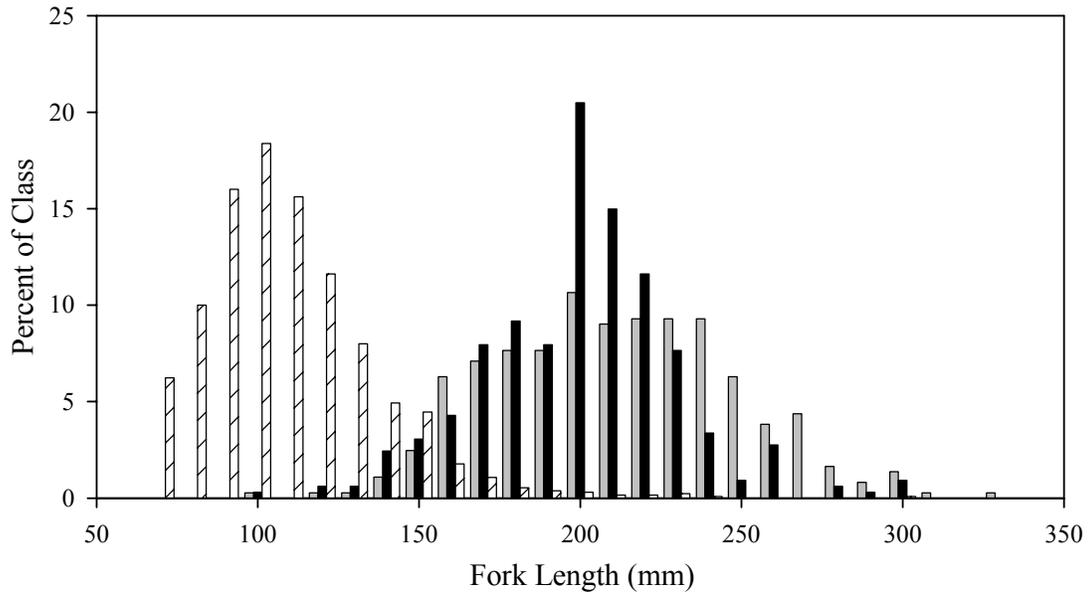


Figure 9. Summed size distribution of all downstream migrants 2002-2004, (n=1300, hashed bars), late fall estuary residents 2002-2005, (n=327, black bars), and back-calculated size at ocean entry of adults returning in 2002-2005, (n=364, grey bars).

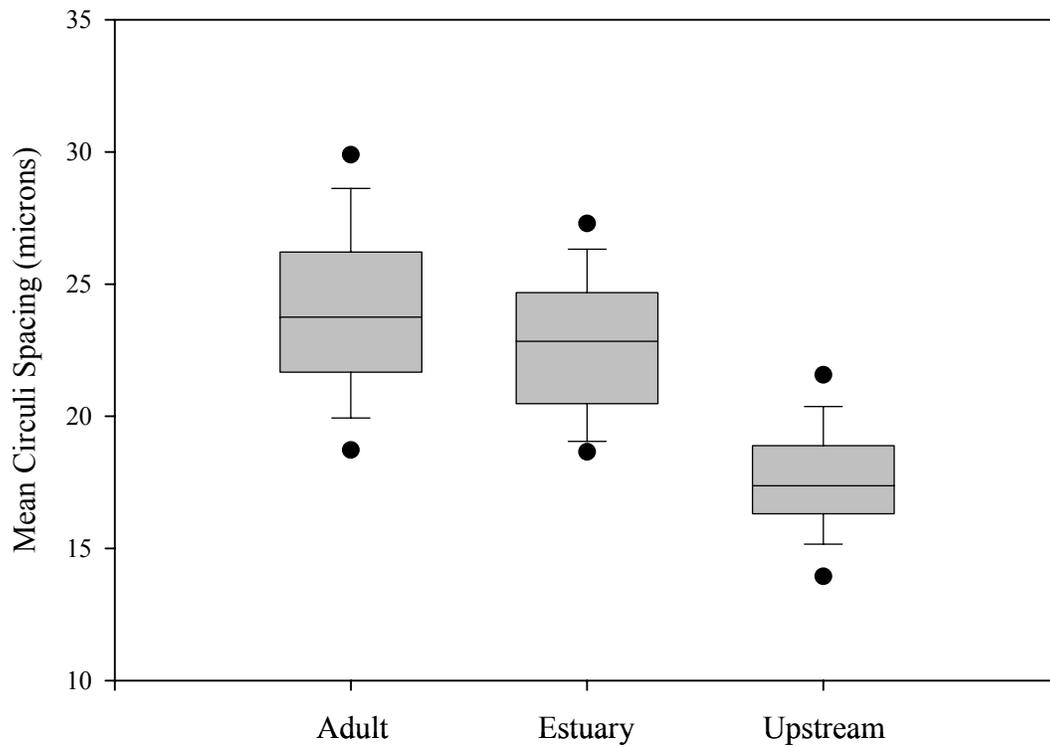


Figure 10. Boxplot depicting the distribution of the mean circuli spacing for the last 18 freshwater circuli for: The freshwater portion of returning adult scales, fall estuary juveniles, and upstream juveniles. Centerline indicates median spacing, while the outer edge of the box indicates the 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles, and dots indicate 5th and 95th percentiles.

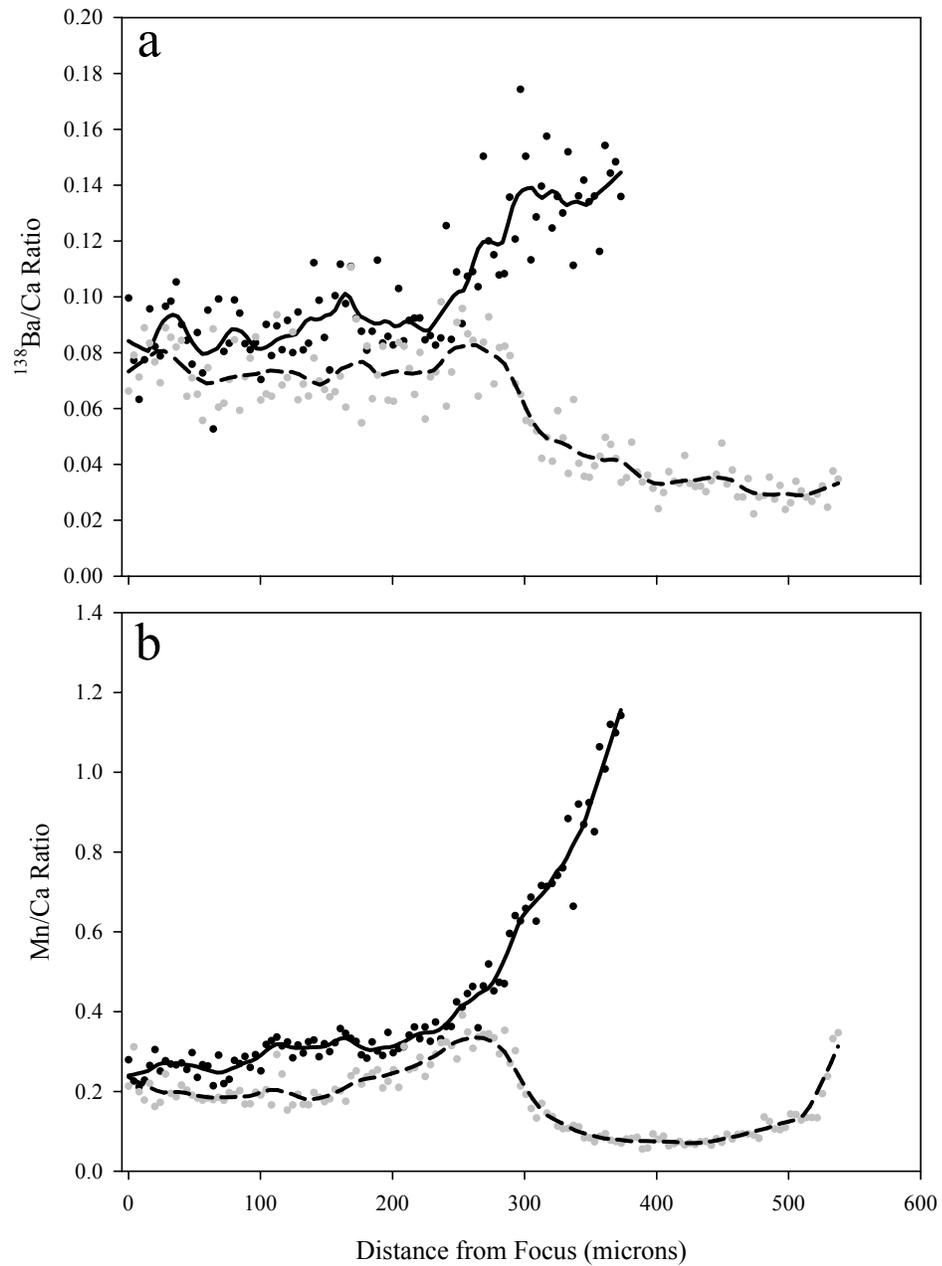


Figure 11. Graphs depicting loess smoothed (a) $^{138}\text{Ba}:\text{Ca}$, and (b) $\text{Mn}:\text{Ca}$ ratios from the focus to the margin on a scale from a juvenile steelhead captured at the downstream migrant trap on 6/22/2004 at 78 mm FL (solid black line), and 78 days later in the estuary at 135 mm FL (dashed line). These data are typical of multiple scales analyzed from pre-and post-estuary entrance.

Appendix A. Numbers of hatchery and wild produced steelhead sampled (i.e. measured, tagged or scales taken) over the course of the study.

Year	Upstream Juveniles		Downstream		Lagoon Juveniles		Adults Sampled	
	Tagged and Sampled		Migrants Sampled		Sampled		Wild	Hatchery
	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery
2002	0	0	455	21	650	8	39	17
2003	270	2	621	10	695	13	51	42
2004	381	2	953	11	473	0	256	104
2005	57	0	235	3	605	3	141	90

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